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EGG CANNIBALISM IN POMACEA CANALICULATA (CAENOGASTROPODA: AMPULLARIIDAE) FROM THE SOUTHERN PAMPAS: AN ALTERNATIVE TROPHIC STRATEGY?

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ABSTRACT

Pomacea canaliculata is a freshwater gastropod native to southern South America and is listed among the world’s 100 worst invaders. Diverse food sources can be exploited by this apple snail, including snails with gelatinous and subaquatic egg masses. Records of ingestion of their own egg masses (egg cannibalism), which are aerial and calcareous, have only been anecdotal in P. canaliculata. Our aims were to study egg cannibalism in a natural population and also under laboratory conditions. In a stream population from the southern Pampas, we recorded P. canaliculata attacking their own fresh egg masses, which had been naturally submerged by an increase in water level. In addition, when we artificially submerged fresh and old egg masses in a field experiment, we observed several snails readily attacking both. In the laboratory, we also observed the capture by pedal surface collecting of floating remains of egg masses. In laboratory trials, juveniles fed on eggs reached larger sizes than starved snails but smaller than those fed on lettuce; adult snails also eat eggs, but their growth rates were not affected by the food regime. Pomacea canaliculata eggs present defensive and anti-nutritive compounds that apparently dissuade almost all potential predators, but this snail did not appear to be negatively affected when feeds on its own eggs. The ingestion of egg remains and submerged egg masses is probably more frequent than previously considered in P. canaliculata, which may take advantage of using these alternative food resources when others are scarce.
Key words: apple snail, invader, intraspecific predation, feeding, growth, pedal surface collecting.

INTRODUCTION

Pomacea canaliculata (Lamarck, 1822) is a
South American apple snail (family Ampullari-
idae) naturally distributed from Paraguay and
southern Brazil southwards to southern Bue-nos Aires Province, Argentina (Martin et al., 2001; Hayes et al., 2012), and it is the only freshwater snail listed among the 100 worst invaders worldwide (Lowe et al., 2000). This species and its congeners inhabit lentic and lotic waterbodies in tropical to warm temperate regions and have invaded several countries around the world, causing important ecologi-cal changes in natural wetlands and economic losses in aquatic agricultural systems (Horgan et al., 2014). A noticeable feature of Pomacea species is the reproductive strategy of deposit-ing masses of eggs with calcareous eggshells

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above the water level on exposed stems, leaves or stones (Heras et al., 1998; Pizani et al., 2005). Underwater predation has been sug-gested as one of the main selective pressures driving the evolution of the aerial egg masses
in apple snails (Snyder & Snyder, 1971; Turner, 1998; Tiecher et al., 2014).
Due to the voracious consumption of macro-phytes by apple snails, they are mainly regard-ed as macrophytophagous, and this habit has been the most intensely studied in ampullariids (e.g., Cowie, 2002; Tamburi & Martin, 2009; Morrison & Hay, 2011b). However, apple snails are able to use different feeding mechanisms to consume a wide spectrum of vegetal and animal resources (Cazzaniga & Estebenet, 1984; Aditya & Raut, 2001; Wood et al., 2006; Kwong et al., 2009; Saveanu & Martin, 2013), including the subaquatic egg masses of other

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freshwater snails (e.g., Cedeño-Leon € Tho-
mas, 1983; Cazzaniga, 1990; Aditya & Raut,
2001, 2002; Kwong et al., 2009).
Intraspecific predation or cannibalism is a
widespread habit that had received little at-
tention up until a few decades ago (Fox, 1975; Polis, 1981). Cannibalism is mainly known in larger individuals that prey on smaller ones or on unprotected life-cycle phases (molting individuals, newborn or eggs). Egg cannibalism has been recorded in almost all groups of ovip-arous animals (Polis, 1981), probably because egg contents and embryos are highly nutritious, easy to capture and seldom toxic (Orians & Janzen, 1974). However, the eggs of Pomacea canaliculata and its congeners are very peculiar in that they present aposematic coloration, they contain different defensive compounds (Heras et al., 2008; Dreon et al., 2010, 2013; Frassa et al., 2010), and they almost lack natural preda-tors (Snyder & Snyder, 1971; Yusa, 2001). All records of egg cannibalism in apple snails have come from the laboratory and are mostly anecdotal (Alonso & Ageitos de Castellanos, 1949; Cazzaniga & Estebenet, 1984; Tiecher et al., 2014), but only one study addressed experimentally the topic (Horn et al., 2008). Although their own eggs cannot be the staple trophic resource for any animal population, egg cannibalism may represent an alterna-tive strategy at the individual level when other resources are scarce or absent. For instance, hatchlings of Arianta arbustorum (Linnaeus, 1758) (Helicidae) only cannibalize conspecific eggs, irrespective of their relatedness, and those that do so increase their chances of reaching maturity (Baur, 1994).
The aims of the present study are to describe and quantify the occurrence of egg cannibalism in P canaliculata in a stream population in the southern Pampas. We also performed labora-tory trials to study the consumption of eggs and egg remains and to determine the effect of this alternative food source on growth rates of juveniles and adults of P. canaliculata.

MATERIALS AND METHODS

Field Observations

During a study of the daily rhythms of pedal surface collecting ina Southern Pampas popu-lation of Pomacea canaliculata (El Huascar stream; 36°55’50”$, 61°35'48"W), ме per-formed systematic observations of surface and

subsurface activities on ten floating quadrats (96 x 48 cm, at 10-30 cm from the shore, along 30 m of the stream) during 27 h (nine observa-tion periods of one hour every three hours); in each observation period two operators recorded the activities in each quadrat (during 1 minute and 45 seconds every 20 minutes; Saveanu & Martin, 2013) three times. On 8 December 2011 at 8:30 AM (ART) we detected a 5 cm increase in water level relative to the previous observation period and the natural submergence of many egg masses deposited on stems of shore plants. During that and sub-sequent observation periods, we recorded the presence of apple snails on the submerged egg masses, making radular and jaws movements on them (Fig. 1).
El Huascar stream (20-25 m wide and 0.2-0.3 m deep) presents a slow current, fairly transparent water and gently sloping banks that allowed us to make observations without dis-turbing the snails’ activities. Water temperature was 25.2 + 4.4°C. Eleocharis bonariensis was the predominant plant and their stems were used by P. canaliculata as substratum for the egg masses. Other snail species present in the stream were Chilina parchappii (d’Orbigny, 1835) (Chilinidae), Biomphalaria peregrina (d’Orbigny, 1835) (Planorbidae) and Physa acuta (Draparnaud, 1805) (Physidae).

Experimental Field Observations

An experiment was performed in El Huascar stream on 28 December 2011, to quantify the occurrence of egg cannibalism and to test for the effect of egg mass freshness. Egg masses from P. canaliculata were obtained in the surroundings of the study site by cutting the stems of Eleocharis bonariensis on which they were laid.
An egg mass was considered fresh when the egg shells and the mucus surrounding them were still soft and moist, indicating that it had been laid during the night before the observa-tion (Turner, 1998; Pizani et al., 2005); an egg mass was considered old (one to seven days old) when the mucus was dry and the egg shell had become hardened but there was no visual evidence of consumption of the pink perivitell-ine fluid by the embryos (Heras et al., 1998). A fresh and an old egg mass were deployed on the stream bottom near each of the ten quad-rats of the pedal surface collecting study. Observations started one hour after the deployment of egg masses and followed the

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FIGS. 1,2. Pomacea canaliculata feeding on its own eggs. FIG. 1: Adult of Pomacea canaliculata attacking an egg mass deposited on Eleocharis bonariensis in El Huáscar stream; FIG. 2: Adult of Pomacea canaliculata capturing Pomacea canaliculata eggs by pedal surface collecting.

same time schedule used for the pedal surface collecting study (Saveanu & Martin, 2013).
During three observation periods, the percent-
age of egg masses of each type attacked was recorded and compared with Fisher’s exact test. At the end of the 27 h of observation, the apple snails below each quadrat were hand-picked. The intensity of egg mass attack during each observation period was estimated as the average number of snails observed in each egg mass divided by the number of snails picked up below that quadrat. Pairwise comparisons (t-test) were performed to compare the inten-sity of the attack between fresh and old egg masses at the 8:30 AMART and 11:30 AMART observation periods.

Feeding on Floating Eggs in the Laboratory

Snails, maintained without food for 24 h, were randomly chosen from a laboratory stock and placed in a glass aquarium at 25°C under natu-ral illumination complemented with artificial light on March 2012. One or ten snails (shell length (SL) 10-50 mm, measured from the apex to the farthest point of the aperture) were put in 12 Land 24 L aquaria, respectively. Remains of hatched egg masses (non-developed pink eggs in clumps or isolated, egg shells and dry hatchlings; Fig. 2) were scattered gently onto the surface. Direct capture by mouth or by

pedal surface collecting (Saveanu & Martin, 2013) and subsequent ingestion were recorded for two hours.

Egg Cannibalism and Growth Rates in the Laboratory

Juvenile and adult snails were fed under three different regimes: no food (0), only eggs (E) and only lettuce (L) to study the effects of egg cannibalism on the growth rates of P canaliculata.
Adults and egg masses of P. canaliculata were collected in El Huascar stream on 9 Feb-ruary 2012. Twenty egg masses (one to seven days old according to their colour, hardness and dryness) were frozen at -18°C in the laboratory. Adults and hatchlings (obtained from six egg masses) were maintained in CaCO3-saturated tap water at 25 + 2°C, under a photoperiod of 12:12 h, and fed fresh lettuce ad libitum. Aquaria were cleaned and the water changed once a week. Thirty hatchlings were reared individually in 200 mL aquaria for two months until they reached a shell length between 14 and 17 mm (juveniles); thirty adults (34-50 mm SL) were maintained in three collective 20 L aquaria for four months.
The experimental regimes were applied to the juveniles and adults for four weeks in individual 3 L glass aquaria under the same conditions

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as before, with the exception that no CaCO;
was added to the water. Each aquarium had a
grid (1.0 mm mesh size) on the bottom to avoid coprophagy. Egg masses were provided in
small pieces (10 to 20 eggs). Known amounts
of lettuce (drained hydrated weight) and eggs (fresh weight) were provided in excess of con-sumption for the experimental snails in L regime and in E regime, respectively.
Every Friday, the aquarium was cleaned and water changed and at the same time the shell length (SL, mm) and live weight (LW, g, weighed after the snail had crawled onto a dry plastic surface) were recorded.
Specific growth rates of SL and LW (SLR, mm.mm-1.day-1 and LWR, 9:9-1-дау-1) were calculated on a weekly basis, as the difference between the final and initial values, divided by the initial value. At the end of each experiment, snails were sacrificed by immersion in water at 100°C and frozen at -18°C for later dissection. The body was extracted from the shell and was dried at 70°C for 48 h, to obtain the body dry weight (BDW, g). The shell and operculum were weighed after 48 h at 70°C to obtain shell dry weight (SDW, g).
At the end of each week, egg remains were collected with a sieve, drained and weighed, to obtain the weight of the consumed eggs; to consider hydration effects the weight of eggs was corrected by a factor obtained from the fresh and drained weight of similar amounts of eggs after a week of submergence in control aquaria without any snails (n = 8). Daily specific ingestion rates (SIR, g-g-1-day-1) were estimated as the weight of consumed eggs divided by LW of each week.
As the four week experiments were not per-formed simultaneously for juvenile and adult snails they were analyzed separately. Pairwise comparisons (t-test) between the initial and final SL and LW were performed between the three regimes (L, E and 0). The specific growth rates (SLR and LWR) and final measurements (SL, LW, BDW and SDW) were compared using ANOVAs; least significant difference (LSD) tests were performed to locate the dif-ferences between regimes. Some variables were transformed after the rejection of Levene’s test of homoscedasticity (p < 0.05); when the no transformation was applicable or effective, Kruskal-Wallis tests were performed followed by t-test for unequal variances between pairs of means.

RESULTS

Field Observations

After the water level rise at 8:30 AM ART, we recorded the submergence of some egg masses. In one out of ten quadrats, we ob-served one apple snail attacking a submerged egg mass. In the following observation (11:30 AM ART), the same egg mass was observed being attacked by up to four apple snails si-multaneously, and in another quadrat an egg mass was also attacked by up to two apple snails. At 2:30 PM ART observation, five and one apple snails, respectively, were observed attacking the same egg masses. The two at-tacked egg masses were fresh, laid early the same night. One of the egg masses was only partially submerged, and part of the snails’ shell and cephalopodium frequently emerged during the attacks (Fig. 1).

Experimental Field Observations

During our observations apple snails of various sizes (25 to 45 mm) were observed attacking the egg masses, mainly fresh ones, within one hour of their submergence. During the first and second observation periods, fresh egg masses were attacked more frequently than the old ones (Fig. 3), although without any significant differences (Fisher’s exact test, 8.30 h, p = 0.370 and 11.30 h, p = 0.474). The fresh egg masses showed signs of disintegra-tion during the first and second observation periods. In the last observation period (2:30 PMART), nine out of the ten fresh egg masses had almost completely disappeared (just a few scattered eggs remained in two of them), and very few snails were detected on the old egg masses (Fig. 4). No significant differences were found between the intensity of egg mass attack on fresh and old egg masses at 08.30 and 11.30 h AM ART (paired t-tests, ty = 1.938, р = 0.085 and ty = 0.853, p = 0.416, respectively). The number of snails simultaneously attack-ing an egg mass ranged from one to six; no attacks were observed by any other snail or fish species. During the 27 h of observation, between 0.13 and 2.60 snails per quadrat were recorded shredding or scraping vegetal material and between 0.00 and 1.13 snails per quadrat were observed performing pedal surface collecting.

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FIGS. 3, 4. Cannibalistic attacks on Pomacea canaliculata egg masses in El Huäscar stream in each observation period. FIG. 3: Percentage of egg masses attacked; FIG. 4: Means of attack intensity (number of snails attacking each egg mass divided by snail density in each quadrat).

Feeding on Floating Egg Mass Remains in
the Laboratory

A few minutes after the snails were placed
on the bottom of the aquarium, they became
active and crawled up to the water surface,
formed funnels with their forefeet and started to collect material from the surface (pedal surface collecting; Fig. 2). The captured material (unhatched eggs, egg shells and

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dry hatchlings) formed a mass with mucus within the funnels and then the snails put their mouths into the funnels and ingested it, using their jaws and radulae. The snails also ingested the egg mass remains without forming any pedal funnels, when they directly contacted the material on reaching the water surface. The snails were observed for a week after the trial and no harmful effects or deaths were recorded.

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FIGS. 5, 6. Means of daily growth rates along the experiment for juveniles of Poma-cea canaliculata under three different food regimes: L: lettuce; 0: no food; E: eggs. Means inside the ellipses were not significantly different (t-test for unequal vari-ances, p < 0.05). FIG. 5: Shell length rate (SLR); FIG. 6: Live weight rate (LWR).

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TABLE 1. Summary of Kruskal-Wallis results for shell length (SLR) and live weight (LWR) growth rates along the experiment for juve-niles of Pomacea canaliculata under three different food regimes.

SLR (mm-mm-1-day-1) LWR (9-9-1-Чау-1)

Week X2 p x p

1 Х2. = 22.826 p<0.001 X2,=25.306 p< 0.001 2 Х2. = 20.179 р<0.001 X2,=20.020 p< 0.001 3 X2,=20.132 p<0.001 X2,=19.676 p< 0.001 4 Х2. = 20.359 p<0.001 X2,=20.921 p< 0.001

Egg Cannibalism and Growth Rates in the food regimes were found (one-way ANOVAs,
Laboratory Fo 27 = 1.285, р = 0.293 and Fo 27 = 1.082, р =
0.353, respectively). The juvenile snails under
None of the snails died during the experiment. the three food regimes, including those starved, No significant differences in initial LW and SL grew significantly in SL and LW after four weeks of the juvenile snails assigned to the different (paired t-tests, p < 0.01). Daily SLR and LWR

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FIGS. 7-10. Back-transformed means (+ 95% CI) of final sizes for juveniles of Pomacea canaliculata under three food regimes: lettuce (L), eggs (Е), no food (0). Different letters indicate significant differ-ences between means (LSD test, p < 0.05). FIG. 7: Shell length (SL); FIG. 8: Live weight (LW); FIG. 9: Shell dry weight (SDW); FIG. 10: Body dry weight (BDW). SL and LW were reciprocally-transformed and SDW and BDW were log, -transformed.

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were significantly different under the three food regimes (Table 1); during the first week, juve-niles feeding on eggs grew two and four times faster, in LW and SL, respectively, compared with unfed snails but less than those feeding on lettuce. In the following weeks, no differ-ences were found between juveniles feeding on eggs and those starved, exception made of LWR in the last week (Figs. 5, 6). After four weeks the final SL and LW showed that the juveniles fed on eggs were significantly larger and heavier (9% and 29%, respectively) than the starved snails, although smaller than those fed on lettuce (Fa2 7 = 308.782, р < 0.001 and F> 27 = 333.617, р < 0.001, respectively; Figs. 7, 8). Both SDW and BDW showed the same pattern with the same significant differences (Fo2 7= 685.084, р < 0.001 and F> 57= 611.119, p < 0.001, respectively, Figs. 9, 10), although the relative differences with starved snails were greater (43% and 46%, respectively).
For adult snails there were marginal differ-ences in initial LW and SL among the snails assigned to the different treatments (one-way ANOVA, Е> 7 = 3.319, р = 0.051 and Fa >57 = 3.161, p = 0.058, respectively); those assigned to the L regime were larger and heavier than those assigned to the E regime (unprotected LSD test, p < 0.05).

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The adults fed with lettuce grew significantly after four weeks but only in LW (paired t-tests, p = 0.035); the adults under the other food re-gimes did not grow either in SL or in LW (paired t-tests, p > 0.200). However, the final SL and LW showed significant differences between different regimes (F297 = 3.677, р = 0.039 and F> 27 = 4.618, р = 0.019, respectively) with the same pattern observed in initial SL and LW values. No significant effect of the food regime was observed for SDW and BDW (Fo2 7 = 0.795, р = 0.462 and Fa >, = 2.961, р = 0.069, respectively).
The daily specific ingestion rates of eggs (SIR, g-g-1-d-1) were higher forj uveniles than for adult snails (Figs. 11, 12). For juvenile snails, an increase in SIR was apparent from the first to the fourth week; the estimated SIR was not significantly different from zero for the first two weeks (probably due to some negative values obtained when the absolute amount of eggs in-gested was very small). On the other hand, SIR was significantly higher than zero during the third and fourth weeks (t-tests, п = 10, р < 0.009 and p < 0.007, respectively). For adult snails, the pattern was not clear, with the estimated SIR being significantly different from zero only
at the second and third weeks (t-tests, n = 10,
р < 0.030 and p < 0.007, respectively).

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FIGS. 11, 12. Box-and-whiskers plot (black line: median; grey box: interquartile range; bar: extreme values) for daily specific ingestion rates of eggs (SIR, 9:9-1-4-1) of Pomacea canaliculata along the experiment. FIG. 11: Juveniles; FIG. 12: Adults.

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DISCUSSION

The observation of attacks of Pomacea ca-
naliculata snails on conspecific egg masses
naturally submerged in the field was recorded
for the first time. Artificially submerged egg
masses were also readily attacked and the fresh ones were mostly disintegrated in the course of a few hours by the feeding attempts of several snails. These attacks were recorded even when vegetal material was available and snails were detected feeding on it. Predation of eggs of other freshwater snails is probably not uncommon behaviour in apple snails (e.g., Cedeño-Leon & Thomas, 1983; Cazzaniga & Estebenet, 1984; Cazzaniga, 1990) including Pomacea species (Aditya & Raut, 2001, 2002). In particular, P. canalicu-lata devoured the egg masses of five differ-ent species of freshwater snails in laboratory experiments (Kwong et al., 2009). In all these studies, the egg masses were gelatinous and subaquatic.
Egg cannibalism is apparently common in Aso-lene pulchella (Anton, 1838), an apple snail that lays gelatinous egg masses underwater (Tiecher et al., 2014). On the other hand, it seems to be rare in apple snails that lay aerial egg masses with calcareous eggshells. Egg cannibalism in aquaria was reported for Pomacea maculata (Perry, 1810) (Alonso & Castellanos, 1949) and P. canaliculata, as noted by Cazzaniga & Estebenet (1984) although it is not clear if it occurred above or under water. We have also observed egg masses partially devoured above water in small aquaria with only one female ora couple ofP . canaliculata (pers. obs.). Females of Pomacea get out of the water to lay eggs 1.4 times a week on average (Albrecht et al., 1996) The above-water attack on egg masses seems to be infrequent, since the probability of an encounter with an egg mass depends on the female getting out of the water in the same place as previously used by herself or by another female.
In our experimental field observations, sub-merged egg masses were not attacked by any other snail species or fish (mostly Jennynsia multidentata) present in the stream. Neither did we observe any attacks from terrestrial animals on Р canaliculata egg masses above the wa-terline. The conspicuously coloured aerial egg masses of Pomacea spp. are seldom attacked by predators, which has been attributed to their unpalatability and aposematic colour (Snyder & Snyder, 1971; Dreon et al., 2010, 2013; Frassa

et al., 2010). Fire ants and some terrestrial snails are some of the few animals that have been observed feeding on Pomacea eggs (Yusa, 2001; Ng & Tan, 2011). On the contrary, Р canaliculata attacked readily and persistently its own egg masses in our laboratory and field experiments, even when other food sources are present; Horn et al. (2008) also mentioned cannibalism of submerged egg masses of P maculata in the presence of lettuce.
Turner (1998) found little evidence of un-derwater predation (including cannibalism) for experimentally submerged egg masses of P paludosa in two Florida lakes. Our field evidence indicates that egg cannibalism is probably not as infrequent in natural popula-tions of P canaliculata in the southern Pampas. Cannibalism of egg masses depends critically on water level fluctuations wide enough to sub-merge them, events that occur frequently but quite unpredictably in lotic waterbodies in the area (Pizani et al., 2005). In addition to water fluctuations, heavy rains, winds and birds may tumble the egg masses or bend their substrates down to the water level. These situations are probably more common in watercourses like El Huascar stream, where practically the only substratum available for egg laying is a very tiny sedge (Eleocharis bonariensis) with thin flexible stems no more than 15 cm tall.
The capture of floating remains of hatched egg masses by pedal surface collecting con-stitutes an alternative mechanism that may be more frequent than direct attacks on submersed egg masses and hence may predispose the snails to attack them whenever possible. Pedal surface collecting is apparently common in P canaliculata though more intense during the night, which probably accounts for the lack of field reports of this behaviour (Saveanu & Martin, 2013). The need to ventilate the lung compels the snails to reach the water surface every 20 minutes at 25°C (Seuffert & Martin, 2009, 2010), which increases the probability of detecting the presence of floating food items. Egg cannibalism only had a significant effect on the growth ofj uvenile snails although adult snails also fed on eggs. Juvenile snails with eggs as the only food item grew more than starved ones, but significantly less than those fed with lettuce ad libitum, indicating that eggs could serve as an alternative trophic resource although of poor nutritive quality. This is odd, as eggs and embryos are usually considered as highly nutritious and energetic food items (Orians & Janzen, 1974). Probably the expla-

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nation of this pattern lies in the anti-nutritive and neurotoxic properties of the perivitelline proteins present in the eggs of Р canaliculata (Dreon et al., 2010, 2013; Frassa et al., 2010). Even though the consequences on size and biomass remained through the duration of the experiment, the positive effect of egg cannibal-ism on growth rate relative to starved snails was mostly significant for the first week. The increase in the egg ingestion rate of juveniles during the experiment was probably due to the increase in the time that they remained without any alternative food but the increased ingestion was apparently balanced by lower assimilation. However, further work is needed to confirm this.
The specific ingestion rates of eggs were around eight times higher forj uveniles than for adult P. canaliculata but this is probably due to an ontogenetic decrease in the specific feed-ing rate already described for shredding and scraping of plant material (Tamburi & Martin, 2009), and pedal surface collecting of floating particulate material (Saveanu & Martin, 2013). The specific ingestion rates of eggs resulted around 100 times lower than those obtained with lettuce for snails of comparable size (Tamburi & Martin, 2009) Defensive second-ary compounds and high dry matter contents reduce the feeding rate of P. canaliculata on macrophytes (Qiu et al., 2009, 2011; Wong et al., 2010; Morrison & Hay, 2011a).
Continued submergence of the egg masses of Pomacea spp. detrimentally affects hatching and developmental rates, although they are able to withstand up to two weeks of submer-gence without a total failure (Turner, 1998; Pizani et al., 2005; Horn et al., 2008; Wang et al., 2012). However, egg cannibalism can change this situation dramatically. Horn et al. (2008) attributed a 99% reduction in hatchling survival to egg cannibalism observed for experi-mentally submerged egg masses of P maculata in aquaria with one adult snail and presence of lettuce. In our field experiment, nine out of ten fresh egg masses disintegrated after seven hours under the simultaneous attack of several (up to six) snails. In the absence of cannibalistic snails in the laboratory, fresh egg masses of P. canaliculata lost their integrity more slowly and more infrequently (nine out of 21 disintegrated spontaneously after submergence periods of at least a day; Pizani et al., 2005). Even if the eggs are not eaten or destroyed by radular movements or chewing, the loose eggs sink to the bottom or are swept by currents and they

would not become exposed to the air if the water level decreased, so they are completely non-viable (Pizani et al., 2005).
Turner et al. (2007) demonstrated that in-traguild egg predation in freshwater snails with subaquatic egg masses may play an important role in the competitive outcome among them. As mentioned above, egg cannibalism was not common in the Florida apple snail, P paludosa, as observed by Turner (1998). However, some wetlands in Florida have been invaded by P canaliculata and P. maculata (Rawlings, 2007; Morrison & Hay, 2011b; EDDMapS, 2013), and so the possibility of interspecific egg predation among these apple snails exists. The evidence gathered indicates that such interactions would be strongly asymmetric for the native snail and detrimental to its hatching rate. The same ef-fects would probably appear on the egg masses of Pila spp., which are laid very close to the waterline (Bahl, 1928; Cowie, 2002), since both Pomacea species have invaded their native wetlands in Southeast Asia.
Egg cannibalism or at least the ingestion of unhatched eggs and egg remains is probably more common in P. canaliculata than previously thought. The attack on egg masses depends mostly on their submergence, but the egg remains and unhatched eggs that naturally fall into the water are trophic items that are probably available during most of the repro-ductive season and for some time afterwards. Whenever P canaliculata snails found egg masses or egg remains, they feed readily on them and, at least the juveniles, benefit in the short term when other trophic resources are absent. This benefit seems to decline with time, but its effects may be long lasting in habitats that are poor in trophic resources. Apple snails seem to be relatively immune to the defensive compounds that deter feeding by most animals on these complex eggs, and during periods of food shortage they may take advantage from energy previously captured by other members of the population.
Negative density-dependent effects have been reported in laboratory and field popula-tions of P. canaliculata and may be responsible of regulation of population size and density (Cazzaniga & Estebenet, 1988; Tanaka et al., 1999: Yoshida et al., 2013). Competition trough food limitation has been seen as the main mechanism underlying these effects (Yoshida et al., 2013), although the very wide trophic spectrum and the different feeding mechanisms would diminish the competitive interactions.

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On the other hand, egg cannibalism may also
play a role in negative density dependence of
P. canaliculata, as suggested for other snails
(Baur, 1988). At high densities, many of the temporarily submersed egg masses of P canaliculata, which would otherwise endure submersion, may be lost with negative con-sequences on recruitment (Horn et al., 2008). Even though in the long term cannibalism cannot be the trophic basis for any animal population, it nevertheless may have important consequences on population dynamics.

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